



# Ployploidy in Asteraceae of the xerophytic scrub of the Ecological Reserve of the Pedregal of San Angel, Mexico City

FABIOLA SOTO-TREJO<sup>1,2\*</sup>, GUADALUPE PALOMINO<sup>1</sup>, JOSÉ LUIS VILLASEÑOR<sup>2</sup> and DANIEL J. CRAWFORD<sup>3</sup>

<sup>1</sup>Laboratorio de Citogenética, Jardín Botánico, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado postal 70-614, 04510 México, D.F., México

<sup>2</sup>Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado postal 70-367, 04510 México, D.F., México

<sup>3</sup>Department of Ecology and Evolutionary Biology and the Biodiversity Institute, University of Kansas, Lawrence, KS 66045, USA

Received 21 April 2012; revised 7 December 2012; accepted for publication 18 June 2013

Asteraceae species diversity is high in the xerophytic scrub of the Ecological Reserve of the Pedregal of San Angel (REPSA), located in the southern part of the Basin of the Valley of Mexico. Here we determined whether the frequency of ployploidy is high in the reserve, given the enhanced ability of ployploids to colonize new habitats. In addition, we compared the frequency of ployploidy in Asteraceae in the reserve with the frequency in three oceanic archipelagos and two continental areas in Mexico. This was done to see how the ‘virtual’ island of the open lava flow in the reserve compares with volcanic islands at different distances from source areas. Chromosome numbers for 75 species of Asteraceae were obtained from published literature. Based on the possession of three or more basic chromosome sets in a nucleus, 33% were ployploids. If taxa with haploid chromosome numbers of  $n \geq 14$  or  $n \geq 11$  were considered to be ployploids, the proportion of ployploids rose to 57 and 75%, respectively. When using a phylogenetic approach, the highest percentage of ployploids (84%) was obtained and it could be inferred whether they are palaeo- or neoployploids; thus, we consider that this criterion better reflects the events of ployploidy in Asteraceae. A high frequency of ployploid species in Asteraceae in REPSA suggests that ployploids may have contributed to the species diversity and the vegetation structure of the xerophytic scrub of this reserve. © 2013 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2013, **173**, 211–229.

**ADDITIONAL KEYWORDS:** chromosome number – Mexico – ployploidy criteria – species diversity – Valley of Mexico Basin.

## INTRODUCTION

Ployploidy, the presence of more than two genomes per nucleus, has played a significant role in the diversification of flowering plants (Stebbins, 1971; Grant, 1981; Leitch & Bennet, 1997; Levin, 2002; Leitch & Leitch, 2008; Soltis *et al.*, 2009). Analyses of cytological and fossil data suggest that 30–70% of all flowering plants are associated with one or more whole genome duplications. Stebbins (1971) estimated that between 30 and 35% of all flowering plants are ployploids

because they have more than two sets of chromosomes. Grant (1963) hypothesized that flowering plants with numbers of  $n = 14$  or higher are of ployploid origin and he postulated that 47% of all flowering plants are ployploid. Goldblatt (1980) postulated that numbers above  $n = 9$  and 10 probably result from a ployploid event in their evolutionary history, and he calculated that at least 70% of monocots are ployploids. Lewis (1980) took an approach similar to that of Goldblatt (1980) with dicots and estimated that at least 70% are ployploids. These estimates are based on suggested low ancestral ( $x = 6–9$ ) chromosome numbers (Ehrendorfer *et al.*, 1968; Stebbins, 1971).

\*Corresponding author. E-mail: fsoto@ibiologia.unam.mx

Because stomatal size is often considerably larger in polyploids than in diploids, Masterson (1994) used comparisons of stomatal size in fossil and extant taxa and estimated that 70% of all angiosperms had experienced polyploidy. Otto & Whitton (2000) used a different approach to estimate the frequency of polyploidy based on the distribution of haploid chromosome numbers in various lineages, and they estimated that c. 2–4% of all speciation events in flowering plants involve polyploidy.

The attributes of polyploids, such as high genetic diversity and heterozygosity, may have both biochemical and ecological benefits that contribute to their success in nature (Soltis & Soltis, 2000; Soltis *et al.*, 2010; but see Martin & Husband, 2009). Polyploids are considered to have enhanced ability to colonize new and/or disturbed habitats as compared with diploids (Stebbins, 1971; Ehrendorfer, 1980; Levin, 1983; Morton, 1993; Lumaret *et al.*, 1997; Soltis & Soltis, 1999). The intrinsic genetic advantages that polyploidy can confer on organisms will be most effective when new habitats are being created and become available for colonization (Morton, 1993). These new habitats may be produced after major geological or climatic events or local catastrophes, including volcanic eruptions and lava flows (Morton, 1993).

About 2000 years ago, a volcanic eruption by the Xitle volcano in the southern part of the Basin of the Valley of Mexico produced major changes in the local environment (Carrillo, 1995). The flow of lava modified the topographical features and shaped both spatial and environmental heterogeneity, allowing for the development of different vegetation types (e.g. pine, fir and oak forests, and xerophytic scrub). The xerophytic scrub community is particularly remarkable, due to both its elevation range (2200–2500 m a.s.l.) and the volcanic soil (Rzedowski, 1954; Carrillo, 1995; Castillo-Argüero *et al.*, 2004). Currently, the xerophytic scrub of the Xitle lava flow has been severely reduced as a result of the urban sprawl of Mexico City. However, it contains high biological diversity that is mainly protected in the Ecological Reserve of the Pedregal de San Angel (REPSA, Fig. 1; Rzedowski 1954; Carrillo 1995; Castillo-Argüero *et al.* 2004, 2009). The flora of the REPSA comprises approximately 377 taxa of vascular plants, 105 (28%) of which are members of Asteraceae (Castillo-Argüero *et al.*, 2009). This high plant richness has been attributed mainly to environmental factors, although it also depends on the specific biological traits of the taxa, such as dispersal and competitive abilities, which may be enhanced by polyploidy (Lumaret *et al.*, 1997; Soltis & Soltis, 1999; Castillo-Argüero *et al.*, 2004, 2009).

Asteraceae (Compositae) are one of the largest and one of the most diverse families of the angiosperms,

with > 23 000 species constituting approximately 10% of flowering plants (Bremer, 1994; Funk *et al.*, 2005). This family shows a diversity of chromosome numbers ranging from  $2n = 4$  in *Brachyscome dichromosomatica* C.R.Carter and *Xanthisma gracile* (Nutt.) D.R.Morgan & R.L.Hartm. [= *Haplopappus gracilis* (Nutt.) A. Gray] to  $2n = c. 432$  in *Olearia albida* Hook.f. (Pinkava & Keil, 1977; Carter, 1978; Beuzenberg & Hair, 1984), and extensive chromosome number has even been reported within taxa (Li *et al.*, 2011). Ancient and recent polyploidy (palaeopolyploidy and neopolyploidy, respectively) have long been hypothesized as the basis for chromosome number evolution in the family and several tribes (Solbrig, 1977; Robinson *et al.*, 1981, 1997; Ito *et al.*, 2000; Stuessy, Weiss-Schneeweiss & Keil, 2004; Barker *et al.*, 2008; Semple & Watanabe, 2009; Smitsen, Galbany-Casals & Breitwieser, 2011).

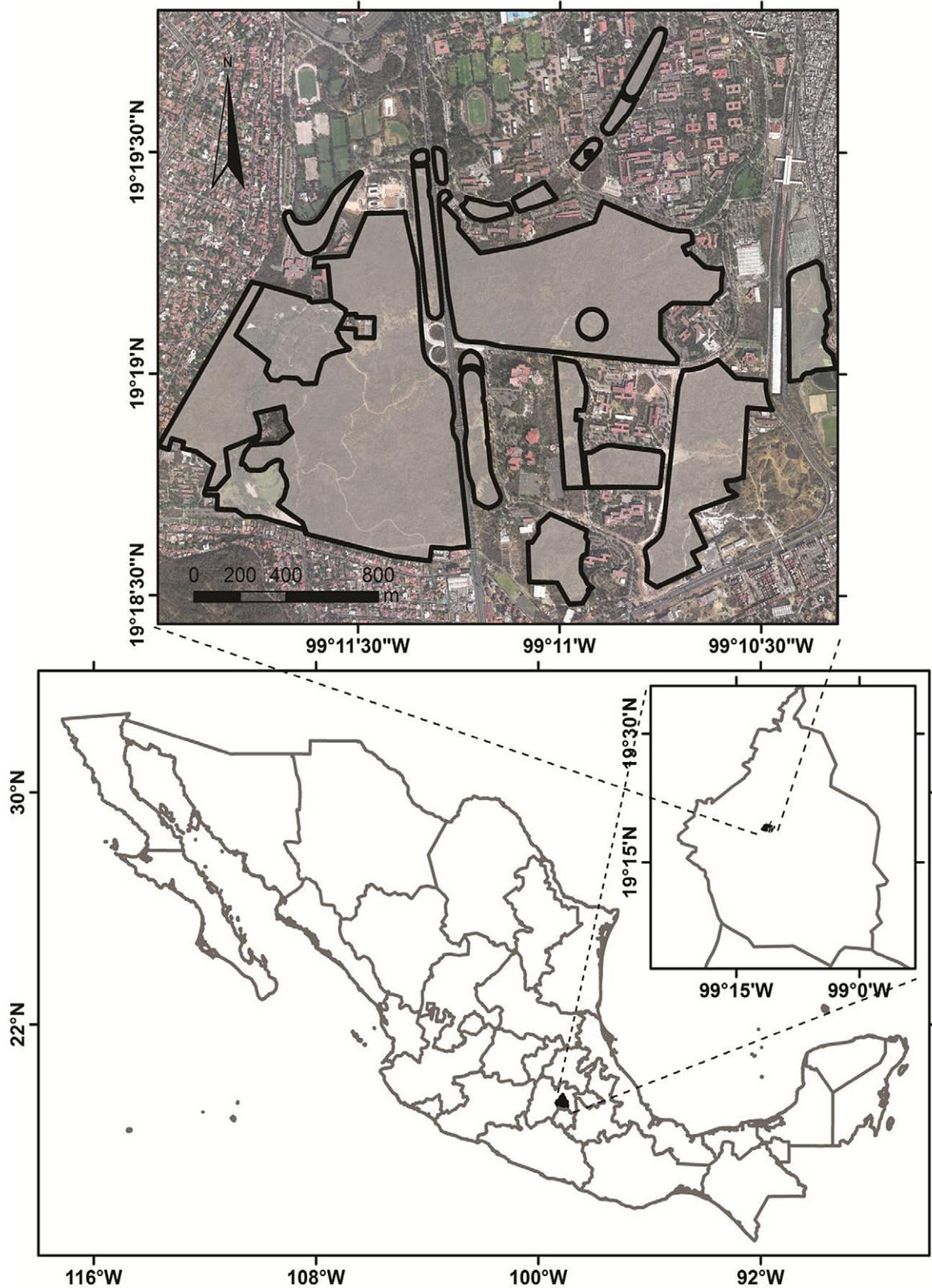
In this review of chromosome numbers for Asteraceae occurring in REPSA, we consider several questions about polyploidy and occurrence of Asteraceae on the reserve. We addressed whether polyploids are more frequent than diploids on the reserve, whether palaeo- or neopolyploids are more frequent, and we wanted to assess the role of polyploids in shaping the Asteraceae community on the reserve. Lastly, we compared the frequency of polyploidy in Asteraceae in the reserve, a 'virtual' island of the open lava flow, with the frequency in three volcanic islands at different distances from source areas; we also included two continental areas to have comparisons with non-island habitats that surround REPSA.

## MATERIAL AND METHODS

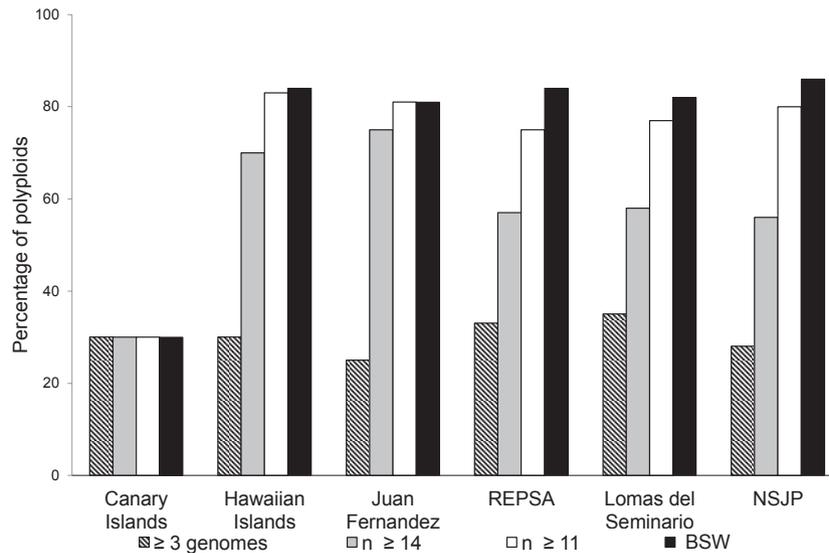
We collected specimens of Asteraceae from 2005 to 2008. The complete collection was identified and deposited at the National Herbarium (MEXU) of the Instituto de Biología, Universidad Nacional Autónoma de México (UNAM).

Chromosome numbers for each taxon were obtained from three different sources, including the literature (Soto-Trejo, Palomino & Villaseñor, 2011), indices of chromosome numbers (Goldblatt, 1981, 1984, 1985), and online indices (Watanabe, 2008, see <http://www.asteraceae.cla.kobe.u.ac.jp/index.html>).

Polyploidy was inferred from chromosome numbers using four different criteria. The first criterion included taxa with three or more chromosome sets ( $2n \geq 3x$ ), where  $x$  represents the base chromosome number in a given genus (Stebbins, 1971). This type of polyploidy results from polyploidization at the infrageneric level (Stebbins, 1971). The second criterion for polyploids was a haploid number of  $n \geq 14$  (Grant, 1963, 1981). The third approach considered



**Figure 1.** Map of the study area. Bottom: Mexico and Mexico City (inset). Top: the Ecological Reserve of the Pedregal of San Angel (REPSA).



**Figure 2.** Distribution of polyploidy of Asteraceae in the selected region.

taxa with haploid number  $n \geq 11$  as polyploids (Goldblatt, 1980).

Finally, we used a combination of the results of Barker *et al.* (2008) and Semple & Watanabe (2009) for creating a fourth criterion, the BSW criterion, which is based on the phylogenetic hypothesis for Asteraceae. Barker *et al.* (2008) analysed the age distribution of duplicate genes from available expressed sequence tag (EST) data to test the presence of palaeopolyploidy in the evolutionary history of Asteraceae and concluded that there had been three episodes of palaeopolyploidy in the evolution of the family. The first whole genome duplication occurred near the origin of the family and prior to the evolution of the tribes. Second and third polyploid events were near the bases of what Barker *et al.* (2008) referred to as tribes Mutisieae and Heliantheae. Semple & Watanabe (2009) superimposed the hypothesized base numbers onto the phylogenetic tree of Asteraceae presented by Funk *et al.* (2005) and they suggested that two polyploid events account for observed chromosome numbers. The results of Barker *et al.* (2008) support the hypothesis of Semple & Watanabe (2009), with the whole genome duplication near the origin of the family, making the entire Asteraceae palaeopolyploid. However, this ancient event is of little interest in the present discussion of polyploidy because of its antiquity. Thus, Mutisieae, Helenieae *sensu stricto* (*s.s.*), Coreopsidae, Neurolaeneae, Tageteae, Chaenactineae, Bahieae, Polymnieae, Heliantheae *s.s.*, Millerieae, Madieae, Perityleae, and Eupatorieae recognized by Funk *et al.* (2005) were hypothesized to be of palaeopolyploid origin (Barker *et al.*, 2008; Semple & Watanabe, 2009).

Under our BSW criterion, we considered palaeopolyploids as those species with a low or high original base number probably derived from pre-existing genera through a past cycle of polyploidy. Examples are: *Melampodium longifolium* Cerv. ex Cav. ( $n = 9$ ,  $x = 9$ , Heliantheae) and *Ageratina cylindrica* (McVaugh) R.M.King & H.Rob. ( $2n = 34$ ,  $x = 17$ , Eupatorieae). Likewise, neopolyploids were interpreted as species having three or more genomes relative to the base number for the tribe, as in *Erigeron karvinskianus* DC. ( $2n = 36$ ,  $x = 9$ , Astereae) and *Roldana sessilifolia* (Hook. & Arn.) H.Rob. & Brettell. ( $2n = 60$ ,  $x = 10$ , Senecioneae). We believe this criterion to be more accurate when compared with the other somewhat subjective criteria in this study, as it is based on a historical framework from molecular phylogenetic analyses (Funk *et al.*, 2005; Semple & Watanabe, 2009). Chromosomal base number for each tribe were obtained from the tree in Semple & Watanabe (2009) (Fig. 3).

The number and percentage of polyploid species were calculated under each criterion for 75 out of 81 species of Asteraceae in REPSA. The frequency of polyploidy in annual and perennial species was calculated and the data were treated with the  $\chi^2$  statistical test. Furthermore, the frequency of polyploidy in Asteraceae in REPSA was compared with the estimates available for the Canary (Crawford *et al.*, 2009), Hawaiian (Carr, 1998) and Juan Fernandez islands (Sanders, Stuessy & Rodríguez, 1983; Kiehn, Jodl & Jakubowsky, 2005), which differ in distances to source areas (95, 3900 and 670 km, respectively; see Table 2). In addition, we compared our study area with two continental areas in Mexico, and also

**Table 1.** Frequency of polyploidy of Asteraceae in the REPSA using four criteria: (a) species with three or more base chromosome number sets (Stebbins, 1971); (b) haploid number  $n = 14$  or more (Grant, 1963); (c)  $n = 11$  or more (Goldblatt, 1980); and (d) BSW

	No. of taxa	$\geq 3$ genomes	$n \geq 14$	$n \geq 11$	BSW	Pal/Neo
All taxa	75	26 (35%)	43 (57%)	56 (75%)	63 (84%)	45%/39%
Taxa endemic to Mexico	19	3 (15.8%)	16 (84.2%)	16 (84.2%)	18 (95%)	63%/32%
Annual taxa	34	10 (29.4%)	12 (35.3%)	22 (62.9%)	26 (76%)	53%/23%
Perennial taxa	41	16 (39.0%)	31 (75.6%)	34 (82.9%)	37 (90%)	41%/49%
* $\chi^2$		0.758	12.350	3.262	2.979	
* $P$		0.38	0.0004	0.07	0.08	

Under 'Pal/Neo', taxa were considered as Pal, palaeopolyploid; or Neo, neopolyploid according to the BSW criterion.

\*Values of the comparison of frequency of polyploidy in annual and perennial species.

obtained calculations for Nuevo San Juan Parangaricutiro (NSJP), a similar habitat resulting from a volcanic eruption by the Parícutín volcano in Michoacán, Mexico (Medina *et al.*, 2000), and with Lomas del Seminario, D.F., México, a habitat next to REPSA (González-Hidalgo, Orozco-Segovia & Diego-Pérez, 2001). The distribution of polyploidy in these regions was analyzed statistically with the  $\chi^2$  test.

## RESULTS

We classified and determined 81 species in 46 genera of Asteraceae in REPSA (Appendix). Most of the taxa belong to highly diversified genera in Mexico, including *Ageratina* Spach, *Baccharis* L., *Bidens* L., *Brickellia* Elliot, *Dahlia* Cav., *Montanoa* Cerv., *Pseudognaphalium* Kirp., *Stevia* Cav., *Verbesina* L. and *Viguiera* Kunth. Other genera, such as *Acourtia* D. Don, *Florestina* Cass., *Pittocaulon* H. Rob & Brettell, and *Roldana* La Llave, are endemic or largely restricted to Mexico. Of the 75 taxa for which chromosome numbers are available, 19 (25.3%) are endemic to Mexico (Appendix). Chromosome numbers are highly variable, ranging from  $2n = 10$  in *Picris echinoides* L. to  $2n = 60$  in *Barkleyanthus salicifolius* (Kunth) H. Rob. & Brettell, *Pittocaulon praecox* (Cav.) H. Rob & Brettell and *Roldana sessilifolia*. Likewise, basic numbers of the genera show a considerable range ( $x = 5, 7, 8, 9, 10, 11, 12, 13, 16, 17, 18, 19, 27$ , and 30).

Based on the possession of three or more base chromosome sets, 26 of these species (34.6%) are polyploids. When taxa with haploid chromosome numbers of  $n \geq 14$  or  $n \geq 11$  were considered to be polyploids, the number of polyploids rose to 43 taxa (57%) and 56 taxa (75%), respectively (Table 1). Using the criteria of Barker *et al.* (2008) and Semple & Watanabe (2009), we obtained the highest percentage of polyploidy (84%) for Asteraceae in REPSA. When polyploidy was examined among endemics to Mexico,

a much higher percentage of polyploids (95%) was obtained with BSW, compared with the percentage of 15.8% obtained with Stebbins' criterion. These results suggest a significant role of polyploidy in the development of this flora.

The frequency of polyploids in annual and perennial species is given in Table 1. The analysis shows that the difference is not statistically significant for species with three or more genomes ( $\chi^2 = 0.758$ ,  $P = 0.38$ ). However, the higher frequency of polyploidy in the perennial species is statistically significant for species with  $n \geq 14$  ( $\chi^2 = 12.350$ ,  $P = 0.0004$ ),  $n \geq 11$  ( $\chi^2 = 3.262$ ,  $P = 0.07$ ) and when we used the BSW ( $\chi^2 = 2.979$ ,  $P = 0.08$ ).

The proportions of polyploids among the selected geographical regions were subjected to the  $\chi^2$  test for comparison. The differences among the regions are statistically significant for all of the criteria (Table 2; Fig. 2). Thus, the distribution of polyploidy appears to be different in each of the regions, even among the continental regions.

## DISCUSSION

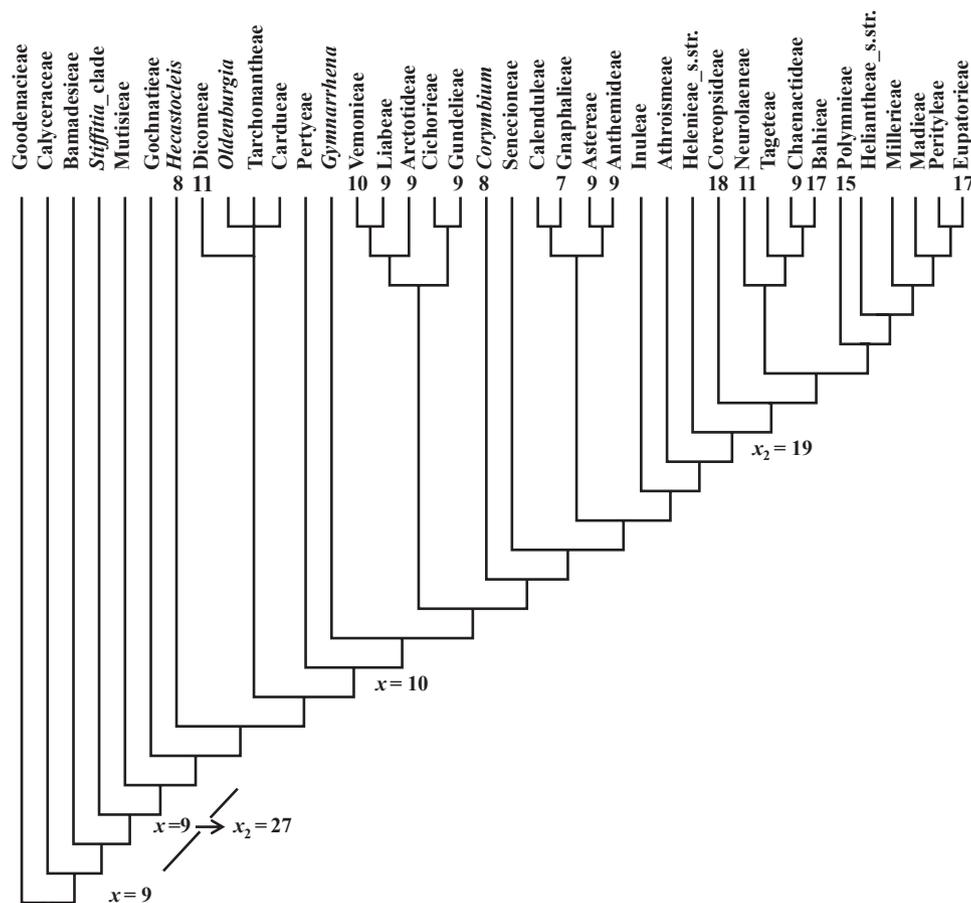
### FREQUENCY OF POLYPLOIDY IN ASTERACEAE IN REPSA

Most estimates of polyploidy have been made using chromosome numbers and different criteria for differentiating between diploids and polyploids. Likewise, estimates of polyploidy in Asteraceae in REPSA vary according to the criterion used to infer polyploidy. The lowest percentage of polyploidy (35%) was obtained with Stebbins' criterion, which is commonly used even though it provides estimates of only recent polyploidy, thus excluding polyploid taxa with high base chromosome numbers that arose from ancient polyploidy events (Goldblatt, 1980). Higher percentages of polyploidy were obtained when using the criteria of Grant (1963, 1981) and Goldblatt (1980) (57 and 75%, respectively).

**Table 2.** Comparison of the frequency of polyploidy of Asteraceae among selected regions

	No. of taxa	$\geq 3$ genomes	$n \geq 14$	$n \geq 11$	BSW (Paleo/Neo)	Reference(s)
Canary Islands	119	30%	30%	30%	30% (0%/30%)	Crawford <i>et al.</i> (2009)
Hawaiian Islands	70	30%	70%	83%	84% (54%/30%)	Carr (1998)
Juan Fernandez Islands	16	25%	75%	81%	81% (0%/81%)	Sanders <i>et al.</i> (1983); Kiehn, Jodl & Jakubowsky (2005)
REPSA	75	35%	57%	75%	84% (45%/39%)	This study
Lomas de Seminario	79	35%	58%	77%	82% (54%/46%)	González-Hidalgo, Orozco-Segovia & Diego-Pérez (2001)
NSJP	142	28%	56%	80%	86% (62%/38%)	Medina <i>et al.</i> (2000)
$\chi^2$		12.467	38.025	98.383	110.337	
$P$		0.0289	< 0.0001	< 0.0001	< 0.0001	

Lomas de Seminario is a continental habitat next to the REPSA, NSJP refers to Nuevo San Juan, Parangaricutiro, which is a habitat formed by a volcanic flow in Michoacán, Mexico.



**Figure 3.** Hypothesized base numbers mapped onto a summary phylogenetic tree of Asteraceae (Funk *et al.*, 2005). Numbers depict basal chromosome numbers; these numbers are found from the base to the tip of a given clade, unless otherwise stated. Notation  $x = 9$   $x_2 = 27$  indicates polyploidy event in these lineages. Modified from Semple and Watanabe, (2009, figure 4.1).

When we used the criteria of BSW, we obtained the highest percentage of polyploidy (84%) for Asteraceae in REPSA. These include both palaeo- and neopolyploids, as defined earlier. Mutisieae and Heliantheae (*sensu* Barker *et al.*, 2008) are palaeopolyploids, but they may also include neopolyploids with whole genome duplications since the ancient polyploid events. Polyploidy in Asteraceae in REPSA is expressed by different kinds of polyploids as follows: (1) taxa with multiples of an original low base number, such as *Conyza* Less. and *Erigeron* L. that include species having somatic numbers of  $2n = 18$ ,  $36$ , base number  $x = 9$ , or *Pseudognaphalium* and *Gamochaeta* Wedd. that include species with somatic numbers of  $2n = 14$ ,  $28$ , base number  $x = 7$ ; and (2) taxa with multiples of a secondary basic number that was itself derived from the original number by an earlier polyploid event, such as *Dahlia*,  $2n = 32$ ,  $64$ ,  $x = 16$  (secondary  $x = 8 + x = 8$ ). Interpretation of the origin of chromosome numbers in Asteraceae may be challenging because they can originate from both ancient and more recent polyploid events (palaeo- and neopolyploidy, respectively), with downward dysploidy following polyploidy to produce lower base numbers (Semple & Watanabe, 2009).

The criteria of Grant (1963, 1981) and Goldblatt (1980) provide a measurement for comprehensive polyploidy, but it is difficult to know from chromosome number alone whether polyploids are of ancient or recent origin. However, using the data of BSW allows a distinction to be made between palaeo- and neopolyploids. When this is done, of the 84% of polyploid Asteraceae in REPSA, 45% are palaeopolyploids and 39% are neopolyploids.

The BSW criterion indicates that palaeopolyploidy occurred in the common ancestor of Eupatorieae, Helenieae, Heliantheae, and Tageteae. Thus, we recognize as palaeopolyploids several genera in REPSA which have high or low base numbers, such as *Ageratina* ( $x = 17$ ), *Ambrosia* L. ( $x = 18$ ), *Bidens* ( $x = 12$ ), *Brickellia* ( $x = 9$ ), *Cosmos* Cav. ( $x = 12$ ), *Florestina* ( $x = 10$ ), *Dahlia* ( $x = 16$ ), *Lagascea* Cav. ( $x = 17$ ), *Melampodium* L. ( $x = 11$ ), *Montanoa* ( $x = 19$ ), *Piqueria* Cav. ( $x = 12$ ), *Simsia* Pers. ( $x = 17$ ), *Stevia* Cav. ( $x = 12$ ), *Tagetes* L. ( $x = 12$ ), *Tithonia* Desf. ( $x = 17$ ), *Verbesina* ( $x = 17$ ), and *Viguiera* ( $x = 17$ ). Molecular and chromosome studies based on evidence from genomic *in situ* hybridization (GISH) have shown that *Dahlia* spp. with  $n = 16$  are allotetraploids combining two similar genomes, originating from hybrids of presently extinct diploids with  $n = 8$  (Gatt *et al.*, 1998; Gatt, Hammett & Murray, 1999). They also suggested that strict bivalent formation in the species with  $2n = 32$  is due to diploidization, which result from intra- and intergenomic reorganization (Martínez & Palomino, 1997; Soltis & Soltis, 1999; Wendel, 2000; Soltis,

Soltis & Tate, 2003; Hegarty & Hiscock, 2005). We also identified some genera such as *Acourtia* ( $x = 27$ ), *Barkleyanthus* H. Rob. & Brettell ( $x = 30$ ), *Pittocaulon* ( $x = 30$ ), and *Roldana* ( $x = 30$ ), which have high base numbers, as neopolyploids. It is evident that polyploidy (palaeo- and neopolyploidy) has played a significant role in the evolution and diversification of Asteraceae (Barker *et al.*, 2008; Semple & Watanabe, 2009). Thus, we emphasize polyploidy based on BSW, because we consider this measure to be a more accurate estimate of polyploidy than the criteria of Stebbins (1971), Goldblatt (1980), and Grant (1963), all of which are based solely on the number of chromosomes.

#### COMPARISONS OF FREQUENCY OF POLYPLOIDY WITH OTHER REGIONS

We compared our findings for Asteraceae in REPSA with the frequency of polyploidy in three oceanic archipelagos and two continental areas (Table 2). Although other factors may influence this comparison, such as island isolation and area, and distance from the source, the xerophytic habitat of REPSA may be considered as an island, given the ecological setting, which is probably the selecting force for the flora in the area. The differences in proportion of polyploids between all six areas were statistically significant based on all four criteria (Table 2), and thus the distribution of polyploidy appears to be heterogeneous.

As shown in Table 2, the frequency of polyploidy in continental regions (Lomas del Seminario and NSJP) is similar to what we found for REPSA when using all criteria for estimating polyploidy. Although our study includes only Asteraceae, the similar incidence in these three regions may indicate a relatively high frequency of polyploidy in the angiosperm flora of Mexico.

The incidence of polyploidy in REPSA (84%) is similar to the Hawai'ian (84%) and the Juan Fernandez (81%) islands, based on BSW. The similar frequency of polyploidy in all these regions may reflect a broader characteristic of polyploid distribution in islands and island-like habitats, such as REPSA. Plant speciation is often associated with polyploidy (Wood *et al.*, 2009), but documentation of the *in situ* origin of polyploids on islands is limited. However, polyploid continental ancestors may enhance the ability for colonizing new habitats after long-distance dispersal because they carry higher genetic diversity in a single diaspore (Sanders *et al.*, 1983; Carr, 1998; Stuessy & Crawford, 1998; Soltis & Soltis, 2000; Crawford *et al.*, 2009). Carr (1998) argued that polyploidy in the Hawai'ian flora reflects mainly palaeopolyploidy inherent in their continental ancestors.

The high incidence of palaeopolyploidy in Asteraceae in REPSA (45%) reflects the fact that about 70% of the studied species belong to palaeopolyploid tribes, such as Eupatorieae, Helenieae, Heliantheae, and Tageteae, which are highly diverse in the vegetation belts around the reserve and we observed a higher proportion of palaeopolyploidy (54%) in Lomas del Seminario, a habitat next to REPSA. Many studies suggest that neopolyploids may offer advantages to the colonizers compared with palaeopolyploids, which may become diploidized with age. By contrast, neopolyploids will have higher genetic diversity and be capable of rapid genetic and genomic changes (Soltis *et al.*, 2003; Pires *et al.*, 2004; Adams & Wendel, 2005). Thus, neopolyploids may have greater potential than palaeopolyploids to colonize and establish in the new habitats in REPSA. Thirty-nine per cent of Asteraceae in REPSA are neopolyploids, a percentage comparable to that which we estimated for the Hawai'ian Islands (30%), and almost identical to the other volcanic-induced habitat in Michoacán (this study, Table 2). In contrast, all polyploid taxa in the Juan Fernandez Islands (81%) are neopolyploids and belong to tribes such as Astereae, Cardueae, Cichorieae, Gnaphalieae, and Senecioneae. Enzyme electrophoresis studies for these successful lineages of the Juan Fernandez and Hawai'ian island floras suggest that the ancestral colonists were neopolyploids (Crawford *et al.*, 2009).

In the Canary Islands, only 30% of Asteraceae are neopolyploids, which is much lower than in the other studied areas. Crawford *et al.* (2009) hypothesized that the proximity of the Canaries to continental source areas could facilitate multiple colonizations, which have increased the genetic diversity in diploid populations. Furthermore, there is a low incidence of polyploidy in the floras of the continental source areas for the Canaries. For example, in tribes such as Cichorieae and Inuleae polyploids are relatively infrequent, and for some genera such as *Atractylis* L., *Carlina* L., *Andryala* L., and *Reichardia* Roth only diploid species are known.

#### THE ROLE OF POLYPLOIDS IN A NEW HABITAT: THE XEROPHYTIC SCRUB OF REPSA

If we consider polyploidy as a potential mechanism for increasing the genetic diversity of colonizers, the high incidence of polyploidy could facilitate the establishment of genetically diverse populations in the newly created environmental conditions after a volcanic eruption in the southern part of the basin of the Valley of Mexico where REPSA is located. The genetic and genomic advantages of polyploidy will be greatest when open habitats are available for colonization and new types of habitats are being created (Morton, 1993).

The Trans-Mexican Volcanic Belt is a mountain chain in which major geological and climatic events have been occurring continuously since its origin in the mid Miocene and probable uplift through the Pleistocene. Thus, the development of this mountain chain may be considered relatively recent (Ferrusquía-Villafranca, González-Guzmán & Cartron, 2005). Since its origin, volcanic activity has been a major feature of this mountain chain, and the potentially catastrophic consequences of this activity could result in a wide range of ecological opportunities through the creation of new habitats.

If we consider that Asteraceae are the largest family in the xerophytic scrub of REPSA, we can infer whether polyploids (palaeo- or neopolyploids) have played a role in the origin and assembly of the vegetation structure found there. Polyploidy has been considered to be more frequent in perennial than in annual plants (Stebbins, 1971). The statistically significant difference in distribution of polyploidy between annual and perennial species of Asteraceae in REPSA is congruent with the views of Stebbins (1971). A high frequency of polyploids in perennial species can be attributed largely to the ability of perennials, once established, to have several seasons of reproduction, in which genetic recombination can produce new genotypes capable of competing successfully for new habitats (deWet, 1980). Also, if the origin of a polyploid goes through a sterile stage (sterile diploid or triploid) perennials, unlike annuals, can exist through generations until fertility is restored. The sterile triploid perennial *Stevia organoides* Kunth ( $2n = 3x = 33$ ) is an example of persistence that could not occur if it were an annual. Thus, perennial habit can be an important factor promoting the establishment of polyploids after colonization (Stebbins, 1971), and most of the examples discussed below are perennial species.

The lava flow from the Xitle volcano promoted the creation of new habitats along an altitudinal gradient of 1000 m, thus allowing contact between plant species from different ecosystems which had the possibility to disperse and colonize these new habitats (Carrillo, 1995). These first invaders were probably polyploids from surrounding habitats (Morton, 1993). Although the colonization process after the eruption of the Xitle volcano is unknown, Carrillo (1995) suggested that *Pittocaulon praecox* was one of the first colonizers of the xerophytic scrub of REPSA. This species is a neopolyploid perennial shrub ( $2n = 60$ ) with particular characteristics for water storage and growing in rocky sites with poor soils, which probably contributed to its success in the area.

Dispersal ability of potential invaders has been also related to polyploidy (Lumaret *et al.*, 1997; Soltis & Soltis, 1999). Examples of neopolyploid species that

we reported for the first time in the REPSA include *Ambrosia confertiflora* DC. ( $2n = 6x = 108$ ) and *Erigeron karvinskianus* ( $2n = 4x = 36$ ). Also, some of the first reports were palaeopolyploids such as *Ageratina brevipes* (DC.) R.M. King & H. Rob. ( $2n = 2x = 34$ ), *Ageratina cylindrica* ( $2n = 2x = 34$ ), *Melampodium longifolium* ( $2n = 2x = 18$ ), and *Montanoa grandiflora* (DC.) Sch. Bip. ex K. Koch ( $2n = 2x = 38$ ) (Soto-Trejo *et al.*, 2011). These species are widely distributed in different habitats in areas surrounding the Distrito Federal, and could be considered as recent invaders. Similarly, Castillo-Argüero *et al.* (2004) noted the recent invasion and establishment of perennial palaeopolyploids such as *Buddleja cordata* Kunth and *B. parviflora* Kunth ( $x = 19$ , Scrophulariaceae).

Another feature positively associated with polyploidy is the abundance of single species in a local flora (Hodgson, 1987; Lumaret *et al.*, 1997). Rzedowski (1954) defined as *Senecionetum praecoxis* the xerophytic scrub in the lava field of the Xitle volcano due to the abundance of *Senecio praecox* DC. (= *Pittocaulon praecox*;  $2n = 60$ ), a dominant neopolyploid species in this area. Other abundant neopolyploids are *Dahlia sorensenii* H.V.Hansen & Hjert. ( $2n = 4x = 64$ ), *Stevia origanoides* and *S. ovata* Willd. ( $2n = 3x = 33$ ). Some perennial palaeopolyploids such as *Ageratina petiolaris* (Moc. ex DC.) R.M.King & H.Rob. ( $2n = 2x = 34$ ), *Cosmos bipinnatus* Cav. ( $2n = 2x = 24$ ), *Dahlia coccinea* Cav. ( $2n = 2x = 32$ ), *Lagascea rigida* (Cav.) Stuessy ( $2n = 2x = 34$ ), *Montanoa tomentosa* Cerv. ( $2n = 2x = 38$ ), and *Verbesina virgata* Cav. ( $2n = 2x = 34$ ) are also abundant species in the area and have been considered as characteristic components (Meave *et al.*, 1994; Castillo-Argüero *et al.*, 2009). Furthermore, other abundant species of other families are perennial neopolyploids, including *Bromus carinatus* Hook. & Arn. ( $2n = 8x = 56$ , Poaceae), *Buddleja cordata* ( $x = 19$ , Scrophulariaceae), *Echeveria gibbiflora* Moc. & Sessé ex DC. ( $2n = 4x = 108$ , Crassulaceae), and *Muhlenbergia robusta* (E.Fourn.) Hitchc. ( $2n = 4x = 40$ , Poaceae) (Stebbins & Love, 1941; Moore, 1947; Reeder, 1968; Uhl, 1992).

The ability to survive in small and isolated populations is a further trait characterizing polyploids (Bayer & Stebbins, 1983; Lumaret *et al.*, 1997). Some perennial neopolyploid species such as *Acourtia cordata* (Cerv.) B.L.Turner ( $2n = 2x = 54$ ), *Barkleyanthus salicifolius* ( $2n = 2x = 60$ ), *Roldana lobata* La Llave ( $x = 30$ ), *R. sessilifolia* ( $2n = 2x = 60$ ), and *Stevia tomentosa* Kunth ( $2n = 3x = 33$ ) and palaeopolyploids such as *Ageratina deltoidea* (Jacq.) R.M.King & H.Rob. ( $2n = 2x = 34$ ), *Tagetes lucida* Cav. ( $2n = 2x = 22$ ), *Verbesina tetraptera* (Ortega) A.Gray ( $2n = 2x = 34$ ), *Viguiera buddlejiformis* (DC.) Benth. &

Hook.f. ex Hemsl. ( $2n = 2x = 34$ ), and *V. excelsa* (Willd.) Hemsl. var. *excelsa* ( $x = 17$ ) are considered as rare species that have persisted as local groups, even after fragmentation and destruction of the habitat in the scrub.

A positive correlation between polyploidy and invasiveness of some plant species was shown by Pandit, Tan & Bisht (2006). We documented that some invasive and introduced plant species have become major weeds in REPSA. Some of the common invasive taxa, such as *Conyza bonariensis* (L.) Cronquist ( $2n = 6x = 54$ ), *Sonchus oleraceus* L. ( $2n = 4x = 32$ ), *Taraxacum officinale* F.H.Wigg. ( $2n = 4x = 32$ ), and *Cirsium vulgare* (Savi) Ten. ( $2n = 4x = 68$ ) are neopolyploids spread over disturbed areas in the vegetation. Likewise, some perennial species of Poaceae are neopolyploids, such as *Chloris gayana* Kunth. ( $2n = 4x = 40$ ), *Melinis repens* (Willd.) Zizka ( $2n = 4x = 36$ ), and *Pennisetum clandestinum* Hochst. ex Chioy. ( $2n = 4x = 40$ ) (Gould & Soderstrom, 1967; Nakagawa, Shumizo & Sato, 1987; Wilen *et al.*, 1995). These non-indigenous species could be leading threats to native biodiversity and the REPSA ecosystem (Castillo-Argüero *et al.*, 2009).

Both palaeo- and neopolyploids may have played a pre-eminent role in the development of the xerophytic scrub of REPSA. Neopolyploids can show rapid changes in gene expression levels, which offer potential advantages to colonizers (Soltis *et al.*, 2010, 2012). The palaeopolyploids could retain genes after duplication events and they could adaptively evolve novel functions, and this might ultimately cause an increase in morphological complexity and biological diversity (Seoighe & Gehring, 2004; Freeling & Thomas, 2006; Jackson & Chen, 2010; Soltis *et al.*, 2010).

The availability of new habitats due to volcanic activity and the close proximity of several vegetation types on the slopes of the mountain in the Pedregal of San Angel have resulted in the evolution of a biologically diverse and unique xerophytic scrub. Polyploids (both palaeo- and neopolyploids) have played a significant role in the assemblage of this flora, by enhancing the invasion, colonization, establishment, and dominance of different plant species in the area (Hodgson, 1987; Morton, 1993; Lumaret *et al.*, 1997; Soltis & Soltis, 2000).

There is a basic difference between the assemblage of the flora of the reserve (a 'virtual island') and the flora of oceanic islands such as the Canaries, Hawai'i and the Juan Fernandez. Oceanic islands tend not to reflect the same balance of taxa as their continental source areas (Carlquist, 1974; Whittaker & Fernández-Palacios, 2007), producing differences between the insular and continental floras. One cause of such contrasting floras is that only good dispersers

in a source flora colonize and establish on oceanic islands. In contrast, in the reserve, dispersal to the lava is probably not limiting and it is the ability to survive in the new environment that is critical. With regard to Asteraceae the area of the reserve is not in disharmony with that of the surrounding area.

The high frequency of polyploid species of Asteraceae in REPSA suggests that polyploids (palaeo- or neopolyploids) may have contributed to the species diversity and the vegetation structure of the xerophytic scrub of REPSA. More information derived from additional chromosome counts and studies of the evolution of the Mexican flora is needed to determine the frequency of polyploid species and the role of polyploidy in species diversification and their ecological distribution in relation to other biological traits (i.e. pollination mode, dispersal mode, growth form, etc.).

#### ACKNOWLEDGEMENTS

We thank Enrique Ortiz, Javier Martínez, and Ingrid Brunner for their technical assistance. Mark Mort and Luis A. Sánchez-González read previous versions of the manuscript and provided valuable comments. F.S.-T. thanks the Posgrado en Ciencias Biológicas (UNAM) for the continuous support throughout this research. This work was supported by Consejo Nacional de Ciencia y Tecnología (CONACYT) through a Masters Dissertation grant (218973) to F.S.-T. Additional funding was provided by PAPIIT-UNAM through a grant (IN214408). We thank three anonymous reviewers and the editors Michael Fay and Ilia Leitch, as all of their comments greatly improved the present paper.

#### REFERENCES

- Adams KL, Wendel JF. 2005. Polyploidy and genome evolution in plants. *Current Opinion in Plant Biology* **8**: 135–141.
- Barker MS, Kane NC, Matvienko M, Kozik A, Michlemore RW, Knapp SJ, Rieseberg LH. 2008. Multiple paleopolyploidizations during the evolution of the Compositae reveal parallel patterns of duplicate gene retention after millions of years. *Molecular Biology and Evolution* **25**: 2445–2455.
- Bayer RJ, Stebbins GL. 1983. Distribution of sexual and apomictic populations of *Antennaria parlanii*. *Evolution* **37**: 555–561.
- Beuzenberg EJ, Hair JB. 1984. Contributions to a chromosome atlas of the New Zealand flora – 27: Compositae. *New Zealand Journal of Botany* **22**: 353–356.
- Bremer K. 1994. *Asteraceae. Cladistics and classification*. Portland, OR: Timber Press.
- Canne JM. 1983. Cytological and morphological observations in *Galinsoga* and related genera (Asteraceae). *Rhodora* **85**: 355–366.
- Carlquist S. 1974. *Island biology*. New York: Columbia University Press.
- Carr DG. 1998. Chromosome evolution and speciation in Hawaiian flowering plants. In: Stuessy TF, Ono M, eds. *Evolution and speciation of island plants*. Cambridge: Cambridge University Press, 5–47.
- Carr DG, King RM, Powell AM, Robinson H. 1999. Chromosome numbers in the Compositae. XVII. *American Journal of Botany* **86**: 1003–1013.
- Carrillo TC. 1995. *El Pedregal de San Angel*. Mexico: Mexico University Press.
- Carter CR. 1978. The cytology of *Brachycome*. 8. The inheritance, frequency and distribution of B chromosomes in *B. dichromosomatica* ( $n = 2$ ), formerly included in *B. lineariloba*. *Chromosoma* **67**: 109–121.
- Castillo-Argüero S, Martínez-Orea Y, Meave JA, Hernández-Apolinar M, Nuñez-Castillo O, Santibañez-Andrade G, Guadarrama-Chávez P. 2009. Flora: susceptibilidad de la comunidad a la invasión de malezas nativas y exóticas. In: Lot A, Cano-Santana Z, eds. *Biodiversidad del Ecosistema del Pedregal de San Angel*. Mexico: University of Mexico Press, 107–133.
- Castillo-Argüero S, Montes-Cartas G, Romero-Romero MA, Martínez-Orea Y, Guadarrama-Chávez P, Sánchez-Gallen I, Nuñez-Castillo O. 2004. Dinámica y conservación de la flora del matorral xerófilo de la Reserva Ecológica del Pedregal de San Angel (D. F., México). *Boletín de la Sociedad Botánica de México* **74**: 51–75.
- Crawford DJ, Lowrey TK, Anderson GJ, Bernardello G, Santos-Guerra A, Stuessy TF. 2009. Genetic diversity in Asteraceae endemic to oceanic islands: Baker's Law and polyploidy. In: Funk VA, Susanna A, Stuessy T, Bayer R, eds. *Systematics, evolution, and biogeography of Compositae*. Vienna: International Association for Plant Taxonomy (IAPT), 101–113.
- Ehrendorfer F. 1980. Polyploidy and distribution. In: Lewis WH, ed. *Polyploidy: biological relevance*. New York: Plenum Press, 45–60.
- Ehrendorfer F, Krendl F, Habeler E, Sauer W. 1968. Chromosome numbers and evolution in primitive angiosperms. *Taxon* **17**: 337–353.
- Ferrusquía-Villafranca I, González-Guzmán LY, Cartron JLE. 2005. Northern Mexico's landscape, part 1. The physical setting and constraints on modeling biotic evolution. In: Cartron JLE, Ceballos G, Felger RS, eds. *Biodiversity, ecosystems, and conservation in northern Mexico*. New York: Oxford University Press, 11–38.
- Freeling M, Thomas BC. 2006. Gene-balanced duplications, like tetraploidy, provide predictable drive to increase morphological complexity. *Genome Research* **16**: 805–814.
- Funk VA, Bayer RJ, Keeley S, Chan R, Watson L, Gemeinholzer B, Schilling E, Panero JL, Baldwin BG, Garcia-Jacas N, Susanna A, Jansen RK. 2005. Everywhere but Antarctica: using a supertree to understand the

- diversity and distribution of the Compositae. *Biologiske Skrifter* **55**: 343–374.
- Gaiser LO. 1953.** Chromosome studies in Kuhniinae (Eupatorieae). I. *Brickellia. Rhodora* **55**: 253–267.
- Gatt M, Ding H, Hammett K, Murray B. 1998.** Polyploidy and evolution in wild and cultivated *Dahlia* species. *Annals of Botany* **8**: 647–656.
- Gatt M, Hammett K, Murray B. 1999.** Confirmation of ancient polyploidy in *Dahlia* (Asteraceae) species using genomic *in situ* hybridization. *Annals of Botany* **84**: 39–48.
- Goldblatt P. 1980.** Polyploidy in angiosperms: monocotyledons. In: Lewis WH, ed. *Polyploidy: biological relevance*. New York: Plenum Press, 219–239.
- Goldblatt P, ed. 1981.** Index to plant chromosome numbers 1975–1978. *Monographs in systematic botany from the Missouri Botanical Garden, vol. 5*. St. Louis: Missouri Botanical Garden, 1–553.
- Goldblatt P, ed. 1984.** Index to plant chromosome numbers 1979–1981. *Monographs in systematic botany from the Missouri Botanical Garden, vol. 8*. St. Louis: Missouri Botanical Garden, 1–427.
- Goldblatt P, ed. 1985.** Index to plant chromosome numbers 1982–1988. *Monographs in systematic botany from the Missouri Botanical Garden, vol. 13*. St. Louis: Missouri Botanical Garden, 1–224.
- González-Hidalgo B, Orozco-Segovia A, Diego-Pérez N. 2001.** La vegetación de la Reserva Ecológica Lomas del Seminario, Ajusco, México. *Boletín de la Sociedad Botánica de México* **69**: 77–99.
- Gould FW, Soderstrom TR. 1967.** Chromosome numbers of tropical American grasses. *American Journal of Botany* **54**: 676–683.
- Grant V. 1963.** *The origin of adaptations*. New York: Columbia University Press.
- Grant V. 1981.** *Plant speciation*. New York: Columbia University Press.
- Grashoff JL, Bierner MW, Northington DK. 1972.** Chromosome numbers in North and Central American Compositae. *Brittonia* **24**: 379–394.
- Hansen HV, Hjerting JP. 1996.** Observations on chromosome numbers and biosystematics in *Dahlia* (Asteraceae, Heliantheae) with an account on the identity of *D. pinnata*, *D. rosea*, and *D. coccinea*. *Nordic Journal of Botany* **16**: 445–455.
- Hegarty MJ, Hiscock SJ. 2005.** Hybrid speciation in plants: new insights from molecular studies. *New Phytologist* **165**: 411–423.
- Hodgson JG. 1987.** Why do so few plant species exploit productive habitats? An investigation into cytology, plant strategies and abundance within a local flora. *Functional Ecology* **1**: 243–250. Index to chromosome numbers in Asteraceae. Available at: <http://www.asteraceae.cla.kobe.u.ac.jp/index.html>
- Ito M, Yahara T, King RM, Watanabe K, Oshita S, Yokoyama J, Crawford DJ. 2000.** Molecular phylogeny of Eupatorieae (Asteraceae) estimated from cpDNA RFLP and its implication for the polyploid origin hypothesis of the tribe. *Journal of Plant Research* **113**: 91–96.
- Jackson S, Chen ZJ. 2010.** Genomic and expression plasticity of polyploidy. *Current Opinion in Plant Biology* **13**: 153–159.
- Jansen RK, Stuessy FT. 1980.** Chromosome counts of Compositae from Latin America. *American Journal of Botany* **67**: 585–594.
- de Jong DCD, Nesom GL. 1996.** Chromosome counts in Mexican *Erigeron*. *Madroño* **43**: 384–392.
- Keil DJ, Luckow MA, Pinkava DJ. 1988.** Chromosome studies in Asteraceae from the United States, Mexico, the West Indies, and South America. *American Journal of Botany* **75**: 652–668.
- Keil DJ, Pinkava DJ. 1976.** Chromosome counts and taxonomic notes for Compositae from the United States and Mexico. *American Journal of Botany* **63**: 1393–1403.
- Keil DJ, Stuessy TF. 1975.** Chromosome counts of Compositae from the United States, Mexico, and Guatemala. *Rhodora* **77**: 171–195.
- Keil DJ, Stuessy TF. 1977.** Chromosome counts of Compositae from Mexico and the United States. *American Journal of Botany* **64**: 791–798.
- Kiehn M, Jodl M, Jakubowsky G. 2005.** Chromosome numbers of angiosperms from the Juan Fernández Islands, the Tristan da Cunha Archipelago, and from mainland Chile. *Pacific Science* **59**: 453–460.
- King RM, Kyhos DW, Powell AM, Raven PH, Robinson H. 1976.** Chromosome numbers in Compositae. XIII. Eupatorieae. *Annals of the Missouri Botanical Garden* **63**: 862–888.
- Leitch AR, Leitch IJ. 2008.** Genomic plasticity and the diversity of polyploid plants. *Science* **320**: 481–483.
- Leitch IJ, Bennett MD. 1997.** Polyploidy in angiosperms. *Trends in Plant Sciences* **2**: 470–476.
- Levin DA. 1983.** Polyploidy and novelty in flowering plants. *American Naturalist* **122**: 1–25.
- Levin DA. 2002.** *The role of chromosomal change in plant evolution*. New York: Oxford University Press.
- Lewis WH. 1980.** Polyploidy in angiosperms: dicotyledons. In: Lewis WH, ed. *Polyploidy: biological relevance*. New York: Plenum Press, 241–268.
- Li W-P, Tang M, Yin G-S, Yin Y, Yang F-S, Chen S-M. 2011.** Extensive chromosome number variation in *Aster ageratoides* var. *pendulus* (Asteraceae). *Botanical Journal of the Linnean Society* **165**: 378–387.
- Lumaret R, Guillermin J, Maillet J, Verlaque R. 1997.** Plant species diversity and polyploidy in islands of natural vegetation isolated in extensive cultivated lands. *Biodiversity Conservation* **6**: 591–613.
- Martin SL, Husband BC. 2009.** Influence of phylogeny and ploidy on species ranges of North American angiosperms. *Journal of Ecology* **97**: 913–922.
- Martínez J, Palomino G. 1997.** Evidence of heterozygous chromosome interchange and chromatid exchange in autotetraploid cytotype of *Gibasis schiedeana* (Tradescantieae-Commelinaceae). *Cytologia* **62**: 275–281.
- Masterson J. 1994.** Stomatal size in fossil plants: evidence for polyploidy in majority of angiosperms. *Science* **264**: 421–423.

- Meave J, Carabias J, Arriaga V, Valiente-Banuet A. 1994.** Observaciones fenológicas en el Pedregal de San Ángel. In: Rojo, A, ed. *Reserva Ecológica 'El Pedregal de San Ángel': Ecología, Historia Natural y Manejo*. Mexico: University of Mexico Press, 91–105.
- Medina C, Guevara-Fefer F, Martínez MA, Silva-Sáenz P, Chávez-Carbajal MA. 2000.** Estudio florístico en el área de la comunidad indígena de Nuevo San Juan Parangaricutiro, Michoacán, México. *Acta Botanica Mexicana* **52**: 5.41.
- Moore RJ. 1947.** Cytotaxonomic studies in the Loganiaceae. I. Chromosome numbers and phylogeny in the Loganiaceae. *American Journal of Botany* **34**: 527–538.
- Moore RJ, Frankton C. 1962.** Cytotaxonomic studies in the tribe Cynareae (Compositae). *Canadian Journal of Botany* **40**: 281–288.
- Morton JK. 1993.** Chromosome numbers and polyploidy in the flora of Cameroons Mountain. *Opera Botanica* **121**: 159–172.
- Mulligan GA. 1959.** Chromosome numbers of Canadian weeds. II. *Canadian Journal of Botany* **37**: 81–92.
- Nakagawa H, Shumizo N, Sato H. 1987.** Chromosome numbers, reproductive method and morphological characteristics of *Chloris* species. *Journal of the Japan Grassland Sciences* **33**: 191–205.
- Olsen J. 1980.** In IOPB chromosome number reports. LXVII. *Taxon* **2**: 346–367.
- Otto SP, Whitton J. 2000.** Polyploid incidence and evolution. *Annual Review of Genetics* **34**: 401–437.
- Pandit MK, Tan HTW, Bisht MS. 2006.** Polyploidy in invasive plant species of Singapore. *Botanical Journal of the Linnean Society* **151**: 395–403.
- Payne WW, Raven PH, Kyhos DW. 1964.** Chromosome numbers in the Compositae. IV. Ambrosieae. *American Journal of Botany* **51**: 418–424.
- Pinkava DJ, Keil DJ. 1977.** Chromosome counts of Compositae from the United States and Mexico. *American Journal of Botany* **64**: 680–686.
- Pires JC, Zhao J, Schranz ME, Leon EJ, Quijada PA, Lukens LN, Osborn TC. 2004.** Flowering time divergence and genomic rearrangements in resynthesized *Brassica* polyploids (Brassicaceae). *Biological Journal of the Linnean Society* **82**: 675–688.
- Reeder JR. 1968.** Notes on Mexican Grasses VIII. Miscellaneous chromosome numbers-2. *Bulletin of the Torrey Botanical Club* **95**: 69–86.
- Robinson H, Carr GD, King RM, Powell AM. 1997.** Chromosome numbers in Compositae XVII: senecioneae. III. *Annals of the Missouri Botanical Garden* **84**: 893–906.
- Robinson H, Powell AM, King RM, Weedin JF. 1981.** Chromosome numbers in Compositae, XII: heliantheae. *Smithsonian Contributions in Botany* **52**: 1–28.
- Rzedowski J. 1954.** Vegetación del Pedregal de San Angel (D. F. México). *Anales de la Escuela Nacional de Ciencias Biológicas* **8**: 59–128.
- Sanders RW, Stuessy TF, Rodríguez R. 1983.** Chromosome numbers from the flora of the Juan Fernandez Islands. *American Journal of Botany* **70**: 799–810.
- Semple JC, Watanabe K. 2009.** A review of chromosome numbers in Asteraceae with hypotheses on chromosomal base number evolution. In: Funk VA, Susanna A, Stuessy T, Bayer R, eds. *Systematics, evolution, and biogeography of Compositae*. Vienna: International Association for Plant Taxonomy (IAPT), 61–72.
- Seoighe C, Gehring C. 2004.** Genome duplication led to highly selective expansion of the *Arabidopsis thaliana* genome. *Trends in Genetics* **20**: 461–464.
- Smitsen RD, Galbany-Casals M, Breitwieser I. 2011.** Ancient allopolyploidy in the everlasting daisies (Asteraceae: Gnaphalieae): complex relationships among extant clades. *Taxon* **60**: 649–662.
- Soejima A, Yahara T, Watanabe K. 2001.** Distribution and variation of sexual and agamosperous populations of *Stevia* (Asteraceae: Eupatorieae) in the lower latitudes, Mexico. *Plant Species Biology* **16**: 91–105.
- Solbrig OT. 1977.** Chromosomal cytology and evolution in the family Compositae. In: Heywood VH, Harborne JB, Turner BL, eds. *The biology and chemistry of the Compositae*. London: Academic Press, 267–281.
- Solbrig OT, Anderson LC, Kyhos DW, Raven PH. 1969.** Chromosome numbers in the Compositae. VII. Astereae III. *American Journal of Botany* **56**: 348–353.
- Solbrig OT, Kyhos DW, Powell AM, Raven PH. 1972.** Chromosome numbers in the Compositae. VIII. Heliantheae. *American Journal of Botany* **59**: 869–878.
- Soltis DE, Albert VA, Leebens-Mack J, Bell CD, Paterson AH, Zheng C, Sankoff D, dePamphilis CW, Wall PK, Soltis PS. 2009.** Polyploidy and angiosperm diversification. *American Journal of Botany* **96**: 336–348.
- Soltis DE, Buggs RJA, Doyle JJ, Soltis PS. 2010.** What we still don't know about polyploidy. *Taxon* **59**: 1387–1403.
- Soltis DE, Mavrodiev EV, Meyers SC, Severns PM, Zhang L, Gitzendanner MA, Ayers T, Chester M, Soltis PS. 2012.** Additional origins of Ownbey's *Tragopogon mirus*. *Botanical Journal of the Linnean Society* **169**: 297–311.
- Soltis DE, Soltis PS. 1999.** Polyploidy: recurrent formation and genome evolution. *Trends in Ecology and Evolution* **14**: 348–352.
- Soltis DE, Soltis PS, Tate JA. 2003.** Advances in the study of polyploidy since plant speciation. *New Phytologist* **161**: 173–191.
- Soltis PS, Soltis DE. 2000.** The role of genetic and genomic attributes in the success of polyploids. *Proceedings of the National Academy of Sciences of the United States of America* **97**: 7051–7057.
- Soto-Trejo F, Palomino G, Villaseñor JL. 2011.** Números cromosómicos de Asteraceae de la Reserva Ecológica del Pedregal de San Angel (REPSA), México, D.F. *Revista Mexicana de Biodiversidad* **82**: 19–29.
- Stebbins GL. 1971.** *Chromosomal evolution in higher plants*. London: Edward Arnold.
- Stebbins GL, Love RM. 1941.** A cytological study of California forage grasses. *American Journal of Botany* **28**: 371–382.

- Strother JL. 1983.** More chromosome studies in Compositae. *American Journal of Botany* **70**: 1217–1224.
- Stuessy TF. 1978.** Revision of *Lagascea* (Compositae, Heliantheae). *Fieldiana Botany* **38**: 75–133.
- Stuessy TF, Crawford DJ. 1998.** Chromosomal stasis during speciation in angiosperms in oceanic islands. In: Stuessy TF, Ono M, eds. *Evolution and speciation of island plants*. Cambridge: Cambridge University Press, 307–324.
- Stuessy TF, Weiss-Schneeweiss H, Keil DJ. 2004.** Diploid and polyploid cytotype distribution in *Melampodium cinereum* and *M. leucanthum* (Asteraceae, Heliantheae). *American Journal of Botany* **96**: 889–898.
- Sundberg S, Cowan CP, Turner BL. 1986.** Chromosome counts of Latin American Compositae. *American Journal of Botany* **73**: 33–38.
- Tomb SA, Chambers KL, Kyhos DW, Powell AM, Raven PH. 1978.** Chromosome numbers in the Compositae. XIV. Lactuceae. *American Journal of Botany* **65**: 717–721.
- Torres AM. 1963.** Taxonomy of *Zinnia*. *Brittonia* **15**: 1–25.
- Turner BL, Ellison WL, King RM. 1961.** Chromosome numbers in the Compositae. IV. North American species, with phyletic interpretations. *American Journal of Botany* **48**: 216–223.
- Turner BL, Flyr D. 1966.** Chromosome numbers in the Compositae. X. North American species. *American Journal of Botany* **53**: 24–33.
- Turner BL, King RM. 1962.** A cytotaxonomic survey of *Melampodium* (Compositae-Heliantheae). *American Journal of Botany* **49**: 263–269.
- Turner BL, King RM. 1964.** Chromosome numbers in the Compositae. VIII. Mexican and Central American species. *Southwestern Naturalist* **9**: 27–39.
- Turner BL, Powell AM, King RM. 1962.** Chromosome numbers in the Compositae. VI. Additional Mexican and Guatemalan species. *Rhodora* **64**: 251–269.
- Uhl CH. 1992.** Polyploidy, dysploidy, and chromosome pairing in *Echeveria* (Crassulaceae) and its hybrids. *American Journal of Botany* **79**: 556–566.
- Watanabe K. 2008.** Index to chromosome numbers in Asteraceae. Available at: <http://www.asteraceae.cla.kobe.u.ac.jp/index.html>
- Watanabe K, King RM, Yahara T, Ito M, Yokoyama J, Suzuki T, Crawford DJ. 1995.** Chromosomal cytology and evolution in Eupatorieae (Asteraceae). *Annals of the Missouri Botanical Garden* **8**: 2581–2592.
- Watanabe K, Yahara T, Soejima A, Ito M. 2001.** Mexican species of the genus *Stevia* (Eupatorieae, Asteraceae). Chromosome numbers and geographical distribution. *Plant Species Biology* **16**: 49–68.
- Wendel JF. 2000.** Genome evolution in polyploids. *Plant Molecular Biology* **42**: 225–249.
- deWet JMJ. 1980.** Origins of polyploids. In: Lewis WH, ed. *Polyploidy: biological relevance*. New York: Plenum Press, 3–15.
- Whittaker RJ, Fernández-Palacios JM. 2007.** *Island biogeography: ecology, evolution, and conservation*. Oxford: Oxford University Press.
- Wilén CA, Holt JS, Ellstrand NC, Shaw RG. 1995.** Genotypic diversity of Kikuyugrass (*Pennisetum clandestinum*) populations in California. *Weed Science* **43**: 209–214.
- Wood TE, Takebayashic N, Barker MS, Mayrose I, Greenspoond PB, Rieseberg LH. 2009.** The frequency of polyploid speciation in vascular plants. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 13875–13879.
- Zhao Z, Turner BL. 1993.** Documented chromosomes numbers 1993: 3. Miscellaneous U.S.A. and Mexican species, mostly Asteraceae. *Sida* **15**: 649–653.

## APPENDIX

Chromosome reports for Asteraceae in the Reserva Ecológica del Pedregal de San Ángel.  $2n$  = somatic chromosome number;  $n$  = gametic or haploid chromosome number;  $x$  = basic chromosome number; 'Ploidy' gives the number of basic chromosome sets contained in the somatic cell nucleus; a species is polyploid if  $2n \geq 3x$  (Stebbins, 1971). Under 'Polyploid', the sign '+' indicates that a species can be regarded as polyploid (either ancient or recent) based on a haploid chromosome number ( $n$ ) exceeding 14 (Grant, 1963, 1981) or 11 (Goldblatt, 1980), respectively. Under 'Neo/Pal', taxa were considered as Neo = neopolyploid or Pal = palaeopolyploid according to hypothesized base numbers mapped onto a phylogenetic tree for Asteraceae presented by Semple & Watanabe (2009). A, annual; P, perennial. A dashed line (–) indicates lack of information on chromosome numbers; these species were not included in the analyses. An asterisk (\*) indicates taxa endemic to Mexico.

Taxa	Collection no.	$n$	$2nC$	$x$	Ploidy	Polyploid ( $n \geq 14$ )	Polyploid ( $n \geq 11$ )	Neo/Pal	A/P	Reference(s)
Anthemideae ( $x = 9$ )										
<i>Artemisia</i>	17, 120, 135,	18		9	4x	+	+	Neo	P	Keil & Stuessy (1975)
<i>  ludoviciana</i>	172									
Nutt.										
Astereae ( $x = 9$ )										
<i>Baccharis</i>	175	9		9	2x				P	Keil & Stuessy (1977)
<i>  heterophylla</i>										
Kunth										
<i>Baccharis</i>	83	–	–	9					P	–
<i>  pteronioides</i>										
DC.										
<i>Baccharis</i>	27	9		9	2x				P	Pinkava & Keil (1977)
<i>  salicifolia</i>										
DC.										
* <i>Baccharis</i>	23,60,181	9		9	2x				P	Keil & Stuessy (1977); Soto-Trejo Palomino & Villaseñor (2011)
<i>  sordescens</i>										
DC.										
<i>Conyza</i>	10, 71, 86	27		9	6x	+	+	Neo	A	Solbrig <i>et al.</i> (1969)
<i>  bonariensis</i>										
(L.) Cronquist										
<i>Conyza canadensis</i>	72	9		9	2x				A	Turner, Powell & King (1962)
<i>  (L.) Cronquist</i>										
<i>Conyza</i>	101 <sup>a</sup>	9		9	2x				A	Keil & Stuessy (1977)
<i>  coronopifolia</i>										
Kunth										
<i>Erigeron</i>	141	9		9	2x				A	Carr <i>et al.</i> (1999)
<i>  delphinifolius</i>										
Willd.										
<i>Erigeron</i>	112		36	9	4x	+	+	Neo	P	de Jong & Nesom (1996)
<i>  karwinskianus</i>										
DC.										
<i>Erigeron longipes</i>	89,93	9		9	2x				P	Sundberg, Cowan & Turner (1986)
<i>  DC.</i>										
<i>Laennecia</i>	8, 87, 94, 96	9		9	2x				A	Carr <i>et al.</i> (1999)
<i>  sophiifolia</i>										
(Kunth)										
G.L.Nesom										
<i>Symphyotrichum</i>	90	5		5	2x				A	Turner, Ellison & King (1961)
<i>  expansum</i>										
(Poepp. ex Spreng.)										
G.L.Nesom										
Cardueae										

APPENDIX *Continued*

Taxa	Collection no.	<i>n</i>	<i>2n</i> C	<i>x</i>	Ploidy	Polyploid ( <i>n</i> ≥ 14)	Polyploid ( <i>n</i> ≥ 11)	Neo/Pal	A/P	Reference(s)
<i>Cirsium vulgare</i> (Savi) Ten.	148		68	17	4x	+	+	Neo	P	Moore & Frankton (1962)
Eupatorieae ( <i>x</i> = 17)										
<i>Ageratina</i> <i>adenophora</i> (Spreng.) R.M.King & H.Rob.	58,84		51	17	3x	+	+	Neo	P	Keil, Luckow & Pinkava (1988)
* <i>Ageratina</i> <i>brevipes</i> (DC.) R.M.King & H.Rob.	163,185		17	17	2x	+	+	Pal	P	Sundberg <i>et al.</i> (1986)
* <i>Ageratina</i> <i>cylindrica</i> (McVaugh) R.M.King & H.Rob.	59,62,63,74, 80,88		34	17	2x	+	+	Pal	P	Soto-Trejo <i>et al.</i> (2011)
* <i>Ageratina</i> <i>deltoidea</i> (Jacq.) R.M.King & H.Rob.	170		34	17	2x	+	+	Pal	P	Grashoff, Bierner & Northington (1972)
* <i>Ageratina</i> <i>oligocephala</i> (DC.) R.M.King & H.Rob.	145, 162, 167, 171, 186			17						
<i>Ageratina</i> <i>pazcuarensis</i> (Kunth) R.M.King & H.Rob.	69,70,77		51I	17	3x	+	+	Neo	P	Grashoff <i>et al.</i> (1972)
* <i>Ageratina</i> <i>petiolaris</i> (Moc. & Sessé ex DC.) R.M.King & H.Rob.	52,56,61,82		17	17	2x	+	+	Pal	P	King <i>et al.</i> (1976)
<i>Ageratum</i> <i>corymbosum</i> Zucc. ex Pers.	127,132		10, 20	10	2x, 4x	+	+	Neo	P	Keil & Stuessy (1975)
<i>Brickellia scoparia</i> (DC.) A.Gray	189		9	9	2x			Pal	P	Gaiser (1953)
* <i>Brickellia</i> <i>secundiflora</i> (Lag.) A.Gray var. <i>secundiflora</i>	38,183,184, 190		9 18	9	2x			Pal	P	Turner & King (1964); Soto-Trejo <i>et al.</i> (2011)
<i>Brickellia</i> <i>veronicifolia</i> (Kunth) A.Gray	40,55,164		9 18	9	2x			Pal	P	King <i>et al.</i> (1976); Soto-Trejo <i>et al.</i> (2011)
* <i>Chromolaena</i> <i>pulchella</i> (Kunth) R.M.King & H.Rob.	101b, 188		– –	10					P	–

APPENDIX *Continued*

Taxa	Collection no.	<i>n</i>	<i>2nC</i>	<i>x</i>	Ploidy	Polyploid ( <i>n</i> ≥ 14)	Polyploid ( <i>n</i> ≥ 11)	Neo/Pal	A/P	Reference(s)
<i>Fleischmannia pycnocephala</i> (Less.) R.M.King & H.Rob.	43,165, 166, 173	20		10	4x	+	+	Neo	P	King <i>et al.</i> (1976); Soto-Trejo <i>et al.</i> (2011)
<i>Piqueria trinervia</i> Cav.	42, 146	12		12	2x		+	Pal	P	Keil <i>et al.</i> (1988)
<i>Stevia micrantha</i> Lag.	153, 174		24	12	2x		+	Pal	A	Watanabe <i>et al.</i> (2001)
* <i>Stevia organoides</i> Kunth	20, 35, 54, 113, 161, 178		33	11	3x	+	+	Neo	P	Soejima, Yahara & Watanabe (2001); Soto-Trejo <i>et al.</i> (2011)
<i>Stevia ovata</i> Willd.	129		22, 33, 44	11	2x, 3x, 4x	+	+	Neo	P	Soejima <i>et al.</i> (2001)
<i>Stevia salicifolia</i> Cav. var. <i>salicifolia</i>	33,45,73	12	24	12	2x		+	Pal	P	Watanabe <i>et al.</i> (1995); Soto-Trejo <i>et al.</i> (2011)
* <i>Stevia tomentosa</i> Kunth	21, 137, 149		33	11	3x	+	+	Neo	P	Watanabe <i>et al.</i> (1995)
<i>Stevia viscida</i> Kunth	142	11	22, 33, 44	11	2x, 3x, 4x	+	+	Neo	P	Watanabe <i>et al.</i> (2001)
Gnaphalieae ( <i>x</i> = 7)										
<i>Gamochaeta americana</i> (Mill.) Wedd	97	14		7	4x	+	+	Neo	A	Carr <i>et al.</i> (1999)
* <i>Pseudognaphalium chartaceum</i> (Greenm) Anderb.	180	14		7	4x	+	+	Neo	A	Keil & Stuessy (1977)
<i>Pseudognaphalium luteo-album</i> (L.) Hilliard & Burt	103	7		7	2x				A	Carr <i>et al.</i> (1999)
* <i>Pseudognaphalium semilanatum</i> (DC.) Anderb.	30	–	–	7					A	–
<i>Pseudognaphalium viscosum</i> (Kunth) Anderb.	102, 123	14		7	4x	+	+	Neo	A	Carr <i>et al.</i> (1999)
Helenieae ( <i>x</i> = 19)										
<i>Florestina pedata</i> (Cav.) Cass.	99	10		10	2x			Pal	A	Keil <i>et al.</i> (1988)
Heliantheae ( <i>x</i> = 19)										
<i>Acmella repens</i> (Walter) Rich.	147	39		13	6x	+	+	Neo	P	Carr <i>et al.</i> (1999)
<i>Ambrosia confertiflora</i> DC.	124	36,54		18	4x, 6x	+	+	Neo	P	Payne, Raven & Kyhos (1964)
<i>Ambrosia psilostachya</i> DC.	104	36		18	4x	+	+	Neo	P	Payne <i>et al.</i> (1964)

APPENDIX *Continued*

Taxa	Collection no.	<i>n</i>	<i>2n<sub>C</sub></i>	<i>x</i>	Ploidy	Polyloid ( <i>n</i> ≥ 14)	Polyploid ( <i>n</i> ≥ 11)	Neo/Pal	A/P	Reference(s)
<i>Bidens bigelovii</i> A.Gray var. <i>angustiloba</i> (DC) Ballard	158		24	12	2 <i>x</i>		+	Pal	A	Olsen (1980)
<i>Bidens odorata</i> Cav. var. <i>odorata</i>	1, 4, 22, 25, 106, 107	12		12	2 <i>x</i>		+	Pal	A	Keil <i>et al.</i> (1988); Soto-Trejo <i>et al.</i> (2011)
<i>Bidens pilosa</i> L.	110	36		12	6 <i>x</i>	+	+	Pal	A	Keil <i>et al.</i> (1988)
<i>Cosmos</i> <i>bipinnatus</i> Cav.	16, 31	12		12	2 <i>x</i>		+	Pal	A	Carr <i>et al.</i> (1999); Soto-Trejo <i>et al.</i> (2011)
<i>Cosmos</i> <i>parviflorus</i> (Jacq.) Kunth	26, 118	12		12	2 <i>x</i>		+	Pal	A	Carr <i>et al.</i> (1999)
<i>Dahlia coccinea</i> Cav.	5, 125	16	32	16	2 <i>x</i>	+	+	Pal	P	Gatt <i>et al.</i> (1998); Soto-Trejo <i>et al.</i> (2011)
<i>Dahlia sorensenii</i> H.V.Hansen & Hjert.	109	32	64	16	4 <i>x</i>	+	+	Neo	P	Hansen & Hjerting (1996); Soto-Trejo <i>et al.</i> (2011)
<i>Galinsoga</i> <i>parviflora</i> Cav.	9, 37, 108	8	16	8	2 <i>x</i>			Pal	A	Canne (1983); Soto-Trejo <i>et al.</i> (2011)
<i>Heterosperma</i> <i>pinnatum</i> Cav.	2, 100	25		13	4 <i>x</i>	+	+	Neo	A	Keil & Stuessy (1975)
<i>Jaegeria hirta</i> (Lag.) Less.	119, 176	18		9	4 <i>x</i>	+	+	Neo	A	Keil & Stuessy (1975)
* <i>Lagascea rigida</i> (Cav.) Stuessy	34, 41, 53, 122	17	34	17	2 <i>x</i>	+	+	Pal	P	Stuessy (1978); Soto-Trejo <i>et al.</i> (2011)
* <i>Melampodium</i> <i>longifolium</i> Cerv. ex Cav.	14, 95, 131, 144, 227	9		9	2 <i>x</i>			Pal	A	Turner & King (1962)
<i>Melampodium</i> <i>perfoliatum</i> (Cav.) Kunth	19, 128, 130a, 230	11		11	2 <i>x</i>		+	Pal	A	Keil & Stuessy (1975)
* <i>Montanoa</i> <i>grandiflora</i> Alamán ex DC.	28, 177	19	38	19	2 <i>x</i>	+	+	Pal	P	Solbrig <i>et al.</i> (1972); Soto-Trejo <i>et al.</i> (2011)
* <i>Montanoa</i> <i>tomentosa</i> Cerv. subsp. <i>Tomentosa</i>	15	19		19	2 <i>x</i>	+	+	Pal	P	Keil <i>et al.</i> (1988)
<i>Parthenium</i> <i>hysterophorus</i> L.	7, 115	17			3 <i>x</i>	+	+	Pal	A	Keil & Stuessy (1977)
<i>Sanvitalia</i> <i>procumbens</i> Lam.	130b, 226	8		8	2 <i>x</i>			Pal	A	Solbrig <i>et al.</i> (1972)
<i>Schkuhria</i> <i>pinnata</i> (Lam.) Kuntze	13, 111	10, 20		10	2 <i>x</i> , 4 <i>x</i>	+	+	Neo	A	Carr <i>et al.</i> (1999); Keil & Stuessy (1975)

APPENDIX *Continued*

Taxa	Collection no.	<i>n</i>	<i>2nC</i>	<i>x</i>	Ploidy	Polyploid ( <i>n</i> ≥ 14)	Polyploid ( <i>n</i> ≥ 11)	Neo/Pal	A/P	Reference(s)
<i>Simsia</i> <i>amplexicaulis</i> (Cav.) Pers.	105, 175	17		17	2x	+	+	Pal	A	Jansen & Stuessy (1980)
<i>Tithonia</i> <i>tubiformis</i> (Jacq.) Cass.	18,	17		17	2x	+	+	Pal	A	Keil & Stuessy (1977); Soto-Trejo <i>et al.</i> (2011)
* <i>Verbesina</i> <i>tetraptera</i> (Ortega) A.Gray	228	17		17	2x	+	+	Pal	P	Turner <i>et al.</i> (1961)
* <i>Verbesina</i> <i>virgata</i> Cav.	24,47	17	34	17	2x	+	+	Pal	P	Turner <i>et al.</i> (1961)
* <i>Viguiera</i> <i>buddlejiformis</i> (DC.) Benth. & Hook.f. ex Hemsl.	143, 168	17		17	2x	+	+	Pal	P	Soto-Trejo <i>et al.</i> (2011)
* <i>Viguiera</i> <i>excelsa</i> (Willd.) Hemsl. var. <i>excelsa</i>	134	–	–	17					P	
<i>Zinnia</i> <i>peruviana</i> (L.) L.	6, 98, 229	12	24	12	2x		+	Pal	A	Torres (1963); Soto-Trejo <i>et al.</i> (2011)
Cichorieae ( <i>x</i> = 9)										
<i>Lactuca</i> <i>serriola</i> L.	91	9	18	9	2x				A	Tomb <i>et al.</i> (1978); Soto-Trejo <i>et al.</i> (2011)
<i>Picris</i> <i>echioides</i> L.	79	5	10	5	2x				A	Keil & Pinkava (1976); Soto-Trejo <i>et al.</i> (2011)
<i>Sonchus</i> <i>oleraceus</i> L.	32	16	32	8	4x	+	+	Neo	A	Turner <i>et al.</i> (1961); Soto-Trejo <i>et al.</i> (2011)
<i>Taraxacum</i> <i>officinale</i> F.H.Wigg.	155		32	8	4x	+	+	Neo	P	Mulligan (1959)
Mutisieae ( <i>x</i> = 9)										
* <i>Acourtia</i> <i>cordata</i> (Cerv.) B.L.Turner	36,44	27	54	27	2x	+	+	Neo	P	Soto-Trejo <i>et al.</i> (2011)
Senecioneae ( <i>x</i> = 10)										
<i>Barkleyanthus</i> <i>salicifolius</i> (Kunth) H.Rob. & Brettell	78, 85	30	60	30	2x	+	+	Neo	P	Turner & Flyr (1966); Soto-Trejo <i>et al.</i> (2011)
* <i>Pittocaulon</i> <i>praecox</i> (Cav.) H.Rob & Brettell	57	30	60	30	2x	+	+	Neo	P	Strother (1983); Soto-Trejo <i>et al.</i> (2011)
* <i>Roldana</i> <i>lobata</i> La Llave	156, 157	–	–	30					P	–

APPENDIX *Continued*

Taxa	Collection no.	<i>n</i>	<i>2nC</i>	<i>x</i>	Ploidy	Polyploid ( <i>n</i> ≥ 14)	Polyploid ( <i>n</i> ≥ 11)	Neo/Pal	A/P	Reference(s)
* <i>Roldana sessilifolia</i> (Hook. & Arn.) H.Rob. & Brettell	133		60	30	2 <i>x</i>	+	+	Neo	P	Zhao & Turner (1993)
Tageteae ( <i>x</i> = 19)										
<i>Dyssodia papposa</i> (Vent.) Hitchc.	29, 136	13		13	2 <i>x</i>		+	Pal	A	Keil <i>et al.</i> (1988)
<i>Tagetes lucida</i> Cav.	114	11		11	2 <i>x</i>		+	Pal	P	Keil <i>et al.</i> (1988)
<i>Tagetes micrantha</i> Cav.	12, 92, 116	12		12	2 <i>x</i>		+	Pal	A	Keil & Stuessy (1975)
<i>Tagetes tenuifolia</i> Cav.	3, 11, 117, 169	24		12	2 <i>x</i>		+	Pal	A	Keil <i>et al.</i> (1988); Soto-Trejo <i>et al.</i> (2011)